

**BIOLOGY AND IMMATURE STAGES OF
LYTOGASTER EXCAVATA, A GRAZER OF BLUE-GREEN
ALGAE (DIPTERA: EPHYDRIDAE)¹**

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Abstract.—Information is presented on the life cycle and larval feeding habits of *Lytogaster excavata* (Sturtevant and Wheeler), a widely distributed species of the ephydrid tribe Hyadini. Larvae are trophically specialized and apparently restricted to feeding on blue-green algae. In northeastern Ohio, the life cycle can be completed in ca. 30 days, and there are probably five generations a year. The egg and mature larva are described and illustrated. The life history strategy of this specialist species is contrasted and compared to that of *Scatella stagnalis* Fallén, a generalist species.

The family Ephydridae, with over 1200 described species distributed in all of the major faunal regions, is one of the largest entities within the acalyprate Diptera (Rohdendorf, 1974). Over 400 species and 68 genera have been recorded from America north of Mexico (Deonier, 1979), and an equally large fauna occurs in the Neotropics (Wirth, 1968). As would be expected in such a large and diverse taxon, considerable adaptive radiation in larval feeding habits has occurred, although the majority of species appear to be microphagous. Larvae are known to utilize a great variety of algae (Brock et al., 1969; Deonier and Regensburg, 1978; Foote, 1979), heterotrophic microorganisms (Eastin and Foote, 1971), and detritus (Busacca and Foote, 1978; Deonier et al., 1979). However, larvae of particular genera have acquired more specialized feeding habits. For example, larvae of *Hydrellia* are leaf miners (Deonier, 1971), those of *Platygyrnopa* utilize decaying snails (Wirth, 1971), *Trimerina* larvae prey on spider eggs (Becker, 1926), and those of *Ochthera* are predators of chironomid and other soft-bodied larvae (Simpson, 1975).

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of Ephydriidae whose larvae utilize blue-green algae (Foote, 1977). At least nine species of the tribe Hyadini of the subfamily Parydrinae have larvae that are associated with colonies of soil-inhabiting blue-green algae occurring in wetland habitats (Foote, 1977). One of the more common hyadine genera reared from field-collected samples of Cyanophyceae has been *Lytogaster*, a genus that currently contains seven species in the Nearctic Region.

The present paper elucidates the life cycle, discusses the larval feeding habits, and describes and illustrates the immature stages of *L. excavata* (Sturtevant and Wheeler), a widely distributed species that has been repeatedly reared from colonies of the genus *Cylindrospermum*.

MATERIALS AND METHODS

Field work was carried out in Arizona, Montana, and Ohio. Most of the information was obtained from studies initiated in Portage County, Ohio, in the northeastern quadrat of the state. Supplementary observations and rearings were obtained in the foothills of the Santa Catalina Mountains near Tucson, Arizona, and along the south shore of Flathead Lake in northwestern Montana.

The laboratory rearings were carried out in an environmental chamber programmed to give a photoperiod of 15L:9D and a temperature of 22°C. ($\pm 1^\circ\text{C}$). Monocultures of most of the algae used in the larval feeding tests were obtained from the University of Texas Culture Collection of Algae (Starr, 1978). Each algal monoculture was established on a nutrient agar substrate in sterile Petri plates, and feeding tests were performed as outlined in Zack and Foote (1978). Monocultures of algae utilized in the tests, along with their UTEX strain numbers, are listed below. Species lacking UTEX numbers were obtained from the Phycology Laboratory at Kent State University.

Cyanophyceae

- Anabaena variabilis* (B-377)
- Anabaena flos-aquae* (1444)
- Anacystis nidulans* (625)
- Cylindrospermum* sp. (LB-942)
- Gloeocapsa alpicola* (B-589)
- Lyngbya* sp. (487)
- Nostoc commune* (584)
- Oscillatoria chalybea* (B-386)
- Oscillatoria tenuis* (B-428)
- Phormidium* sp. (1540)
- Synechococcus leopoliensis* (625)

Chlorophyceae

Chlamydomonas sp.*Chlorella vulgaris* (29)*Cosmarium botrytis* (175)

Bacillariophyceae

Navicula pelliculosa (668)

Chrysophyceae

Botrydiopsis alpina (295)*Botrydium becherianum* (158)

LIFE HISTORY

Adults of *L. excavata* have been swept primarily from shoreline and marshy habitats containing herbaceous vegetation. Deonier (1965) reported this species as occasional in the limnic-wrack, marsh-reed, and sedge-meadow habitats and rare in the sand-shore habitat in Iowa. In northeastern Ohio, Scheiring and Foote (1973) recorded it as abundant in sedge meadows, occasional on limnic wrack and muddy shores, and rare on sandy shores.

The flight period extends throughout the warm season. Adults have been taken as early as mid-May and as late as early October in northeastern Ohio. The overwintering stage is unknown, but many species of Ephydriidae overwinter as adults.

Field-collected adults survived up to 25 days in the laboratory, whereas reared individuals rarely lived more than 20 days. Females had the greater longevity, typically outliving the males by 5–10 days. In laboratory rearing chambers, adults lived for several days in cultures of the blue-green algae *Anabaena* and *Cylindrospermum*, but died within 3–5 days when provided with a monoculture of *Chlorella*. Adults have been observed in nature applying their mouthparts to surfaces of colonies of *Cylindrospermum*, and gut samples of field-collected imagines usually contained numerous trichomes of that genus.

The premating period varied from 3–5 days ($n = 6$) if males were continuously available in the breeding jars. The preoviposition period was somewhat more variable, ranging from 5–10 days ($n = 6$) under laboratory conditions. No overt courtship displays were observed, and mating seemed to be of the "assault" type (Spieth, 1974) in which males attempt to mate with any suitably sized individual.

Mating was observed in a pair of adults collected in a sedge meadow bordering the south shore of Flathead Lake, Montana. The pair was confined to a large petri dish that contained a monoculture of *Cylindrospermum*. When first observed the male was "riding" the relatively immobile female,

being dorsad and parallel to her body. His front tarsal claws were hooked over the anterior edge of her oral cavity. Her wings were spread at about a 45° angle from the longitudinal axis of the body. After 55 seconds, the male moved posteriorly, assumed a nearly vertical position, and grasped the female's genitalia with his claspers. During copulation, his front tarsi repeatedly stroked the anterior surface of the female's mesonotum and the posterior portion of her head. His midtarsi were hooked over the wing bases of the female's divergent wings, while his hind tarsi were loosely appressed to the venter of the female's abdomen slightly anterior to the genital segments. Copulation lasted less than 60 seconds after which the male broke genitalic contact and moved forward to reassume the "riding" position. This alternation of positions occurred three times within a five minute time period before the male decamped.

Four recently mated females were placed for 24-hour periods in petri dishes containing monocultures of algae to determine whether particular algal cultures were more suitable as oviposition sites. Numerous eggs were obtained in cultures of *Anabaena*, *Cylindrospermum*, *Lyngbya*, *Nostoc*, and *Oscillatoria*, but only two eggs were deposited in a *Navicula* plate, and no oviposition occurred in a culture of *Chlorella*. In contrast to the laboratory results, eggs in nature were found only on growths of *Cylindrospermum*, even though numerous colonies of other soil-inhabiting blue-green algal genera were examined. No eggs or larvae were found on colonies of *Anabaena*, *Lyngbya*, *Nostoc*, or *Oscillatoria* that occurred in habitats containing females of *L. excavata*. An additional example of host selectivity by ovipositing females was the discovery of several eggs and larvae of *L. excavata* on a small colony of a species of *Cylindrospermum*, whereas only immature stages of another hyadine species, *Axysta cesta* (Haliday), were found on a growth of *Lyngbya* occurring within 12 cm of the *Cylindrospermum*. Both types of algae were growing on sodden, decaying leaves and soil at the margin of a partly shaded woodland pool. Females of *L. excavata* apparently restrict their oviposition in nature to patches of the host alga, as no eggs were found on moist substrates surrounding an algal colony. A similar selectivity was noticed among females confined to petri plates containing monocultures of blue-green algae. Less than 5% of the eggs were placed on the agar surface itself; most were deposited on the denser algal growths. Eggs were scattered over the surface of the algal colonies or were slightly imbedded. No clustering of eggs was noticed, and they appeared to be deposited singly.

Although exact data were not obtained, some information on the fecundity of individual females is available. A female collected on May 5, 1977, near Kent, Ohio, deposited a total of 34 eggs before dying on May 31. Another female collected on the same date produced 32 eggs before expiring on May 27. The potential fecundity undoubtedly exceeds these values. A field-col-

Table 1. Results of larval feeding tests for *L. excavata* using different algal monocultures.

Alga	Percent Reaching Different Life Stages				
	n	2L	3L	P	A
Cyanophyceae					
<i>Anabaena flos-aquae</i>	30	100	100	20	0
<i>Anabaena variabilis</i>	20	75	70	70	70
<i>Anacystis nidulans</i>	10	0	0	0	0
<i>Cylindrospermum</i> sp.	30	57	47	47	40
<i>Gloeocapsa alpicola</i>	10	0	0	0	0
<i>Lyngbya</i> sp.	10	80	80	80	0
<i>Nostoc commune</i>	10	70	0	0	0
<i>Oscillatoria chalybea</i>	30	0	0	0	0
<i>Oscillatoria tenuis</i>	30	30	0	0	0
<i>Phormidium</i> sp.	30	77	63	33	30
<i>Synechococcus leopoliensis</i>	30	0	0	0	0
Chlorophyceae					
<i>Chlamydomonas</i> sp.	20	0	0	0	0
<i>Chlorella vulgaris</i>	30	0	0	0	0
<i>Cosmarium botrytis</i>	10	0	0	0	0
Bacillariophyceae					
<i>Navicula pelliculosa</i>	30	0	0	0	0
Xanthophyceae					
<i>Botrydiopsis alpina</i>	10	0	0	0	0
<i>Botrydium becherianum</i>	10	0	0	0	0

lected female that was dissected in the laboratory possessed 20 and 21 ovarioles in the two ovaries, respectively. Each ovariole possessed one mature egg, implying a potential fecundity of at least 40 eggs.

The incubation period varied between two and three days and averaged 58 hours ($n = 12$). Newly hatched larvae quickly began feeding on the algal substrate in the immediate vicinity of the eggs.

The results of larval feeding tests using monocultures of 17 species of four classes of algae are presented in Table 1. Larvae completed development and eventually produced adults in cultures of *Anabaena variabilis*, *Cylindrospermum* sp., and *Phormidium* sp., but failed to complete development on *Anabaena flos-aquae*, *Anacystis nidulans*, *Gloeocapsa alpicola*, *Lyngbya* sp., *Nostoc commune*, *Oscillatoria chalybea*, *O. tenuis*, *Chlamydomonas* sp., *Chlorella vulgaris*, *Cosmarium botrytis*, *Navicula pelliculosa*, *Botrydiopsis alpina*, and *Botrydium becherianum*. Eight of ten larvae formed puparia in the *Lyngbya* plates, but failed to produce adults. Somewhat similarly, 20 of 30 newly hatched larvae that were placed in a culture of *A. flos-aquae* eventually reached the third instar but then failed to form

Table 2. Developmental times for *L. excavata* on different algal monocultures.

Alga	Larval Period		Pupal Period		Combined Period	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
<i>Anabaena variabilis</i> (n = 18)	12.3	2.53	14.0	1.94	26.2	3.83
<i>Cylindrospermum</i> sp. (n = 9)	12.3	0.87	11.1	2.37	23.4	3.01
<i>Phormidium</i> sp. (n = 9)	22.3	2.10	18.4	3.95	40.7	4.99

puparia, even after 17 days in the third stadium. In contrast, cultures of the remaining algae apparently were completely unsuitable nutritionally, as all larvae died while still in the first or second stadium.

Differences in the larval and pupal developmental periods were noted even among the algae that were suitable larval foods (Table 2). Thus the combined larval-pupal period was nearly doubled in larvae that were reared on *Phormidium* compared to those that fed on *Anabaena* or *Cylindrospermum*.

The larval period ranged from 11–13 days and averaged 12.3 days when larvae were reared on *Cylindrospermum*. This period was somewhat more variable when *Anabaena* was the larval food, ranging from 10–19 days ($\bar{x}$ = 12.3). In contrast to larvae of many other species of Ephydriidae (Eastin and Foote, 1971; Foote and Eastin, 1974; Deonier and Regensburg, 1978), those of *Lytogaster* usually fed on the surface of the algal colony and made little effort to bury themselves into the substrate, although a few strands of algae commonly were scattered over the dorsal surface of a larva. Larvae feeding within an algal colony moved about very little and seemed quite sluggish compared to other ephydrid larvae. However, larval activity increased significantly when the algal substrate was largely consumed. Larvae established on algal monocultures in petri dishes freely moved to other colonies once the original colony became depleted. Third-instar larvae survived 5–6 days without food, whereas the earlier instars survived only 2 or 3 days.

Table 3. Life cycle data for *L. excavata* in northeastern Ohio. All rearings were maintained at 22°C, with *Cylindrospermum* sp. serving as the adult and larval food.

Flight Period	Mid-May to Late October
Premating Period	3–5 days
Preoviposition period	5–10 days
Incubation period	2–3 days
Larval period	11–13 days
Pupal period	8–13 days
Adult longevity	Ca. 25 days
Fecundity	30 ± eggs/female

Larvae frequently fed together on an algal colony, seemingly without mutual interference. As many as six nearly mature larvae were found in nature on a nearly circular patch of *Cylindrospermum* having a diameter of approximately 3.0 cm. Near Tucson, Arizona, 47 larvae were found in a Petri dish (2.84 cm²) sample of a colony of *Cylindrospermum* growing on moist sand. Larvae of *Lytogaster* commonly occurred together with those of other species of Hyadini. In northeastern Ohio, the associated species were *Hyadina binotata* (Cresson) and, occasionally, *Pelina truncatula* Loew. In southcentral Arizona, larvae of *Lytogaster* were associated with those of *H. binotata* and *P. truncatula*. In all, nine species of Hyadini have been reared from field-collected colonies of *Cylindrospermum* (Foote, 1977).

Approximately 24 hours prior to forming puparia, larvae ceased feeding and moved to slightly higher areas of the algal colony. Puparia were buried in the algal substrate except that the anterior and posterior spiracles typically were exposed to ambient air. The pupal period for larvae that had fed on *Cylindrospermum* in laboratory cultures ranged from 8–13 days and averaged 11.1 days ($n = 9$). In contrast, pupae formed by larvae that had fed on *Phormidium* developed much more slowly, requiring an average of 18.4 days (Table 2).

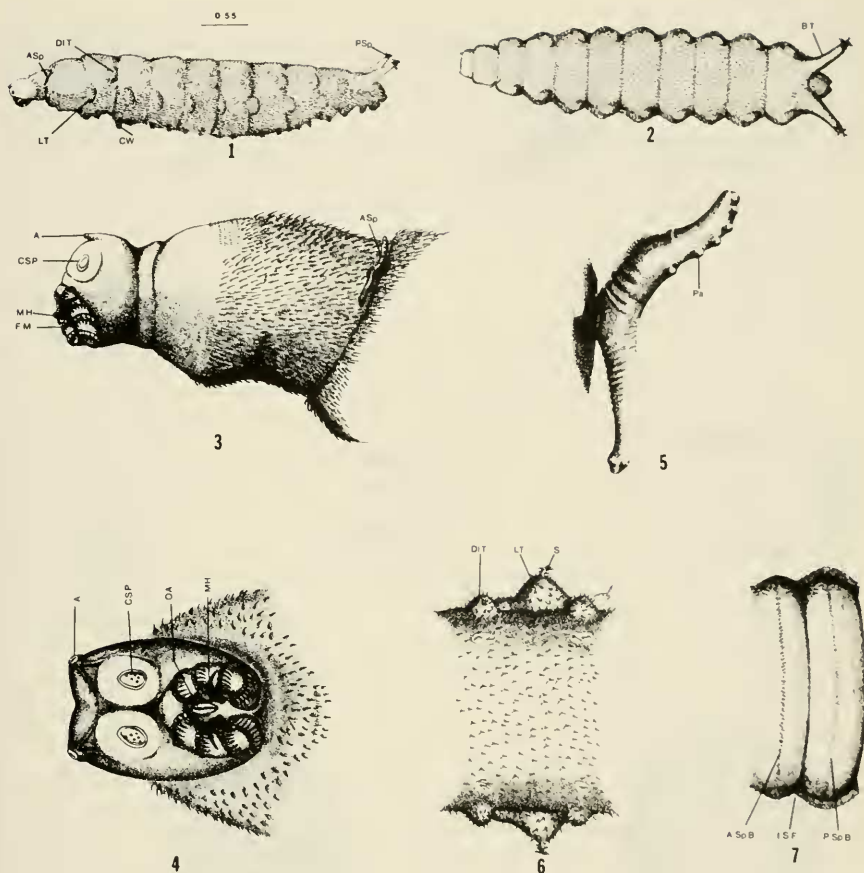
Under laboratory conditions using either *Anabaena* or *Cylindrospermum* as larval food, the life cycle could be completed in approximately 30 days (Table 3). This suggests that 5–6 generations could be produced in northeastern Ohio during a warm season that extends from mid-May to late October (175 days). Adults and larvae were found in nature during February in southern Arizona, suggesting that there is a more or less continuous cycling of generations in more southerly latitudes.

DESCRIPTIONS OF IMMATURE STAGES

Egg (Fig. 15).—Length 0.46–0.54 mm, $\bar{x} = 0.51$; width 0.19–0.23 mm, $\bar{x} = 0.22$ ($n = 10$). Ovoid, more curved ventrally than dorsally. White. Chorion mostly striated; micropylar end upturned and without longitudinal striations, bearing low encircling ridge; opposite end bluntly rounded, slightly upturned but lacking encircling ridge.

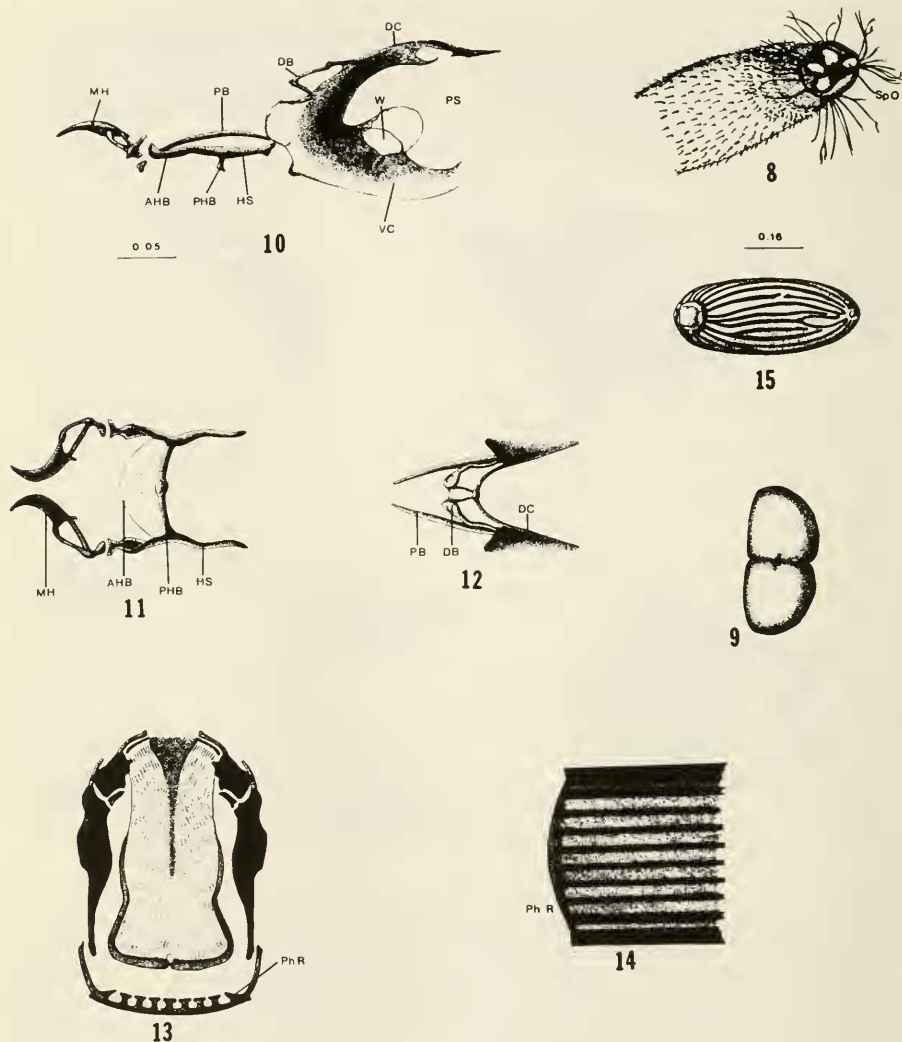
Mature third-instar larva (Figs. 1, 2).—Length 4.2–5.2 mm, $\bar{x} = 4.6$; width 0.70–1.10 mm, $\bar{x} = 0.81$ ($n = 5$). Somewhat flattened dorsoventrally; anterior end tapering, posterior end terminating in 2 strongly diverging breathing tubes borne at apicolateral margins of segment 12; margins of body indented forming double row of low tubercles along length of larva. Integument with numerous pale to blackened hairs.

Segment 1 (pseudocephalic) (Fig. 3) frequently invaginated, bearing antennae apicodorsally, circular sensory plates apicoventrally, and facial mask ventrally; antennae appearing 2-segmented, with both segments wide and



Figs. 1-7. *Lytogaster excavata*, third-instar larva. 1, Lateral habitus. 2, Dorsal habitus. 3, Lateral view of anterior end. 4, Facial mask. 5, Anterior spiracle. 6, Dorsal view of segment 9. 7, Ventral view of segment 9. Abbreviations: A = antenna; ASpB = anterior spinule band; ASp = anterior spiracle; BT = breathing tube; CSP = circular sensory plate; CW = creeping welt; DIT = dorsolateral tubercle; FM = facial mask; ISF = intrasegmental fold; LT = lateral tubercle; MH = mouthhooks; OA = oral aperture; Pa = papilla; PSpB = posterior spinule band; S = sensillum.

short; circular sensory plates with bordering rims complete, each plate with few peg-like structures; facial mask (Fig. 4) with 4 distinct rows of comblike structures on each side of oral aperture, each row consisting of narrow basal piece bearing 7-10 tapering teeth along posterior margin, rows somewhat curved. Segment 2 (prothoracic) spinulose, bearing bifurcate anterior spiracles posterolaterally (Fig. 3); each spiracle (Fig. 5) with 2 strongly diverging branches, upper branch bearing 5-7 papillae along anterolateral surface, lower branch with 3 subapical papillae; base of spiracle arising from



Figs. 8-14. *Lytogaster excavata*, third-instar larva. 8. Posterior spiracle. 9. Perianal pad. 10. Lateral view of cephalopharyngeal skeleton. 11. Ventral view of hypostomal sclerite and mouthhooks. 12. Dorsal view of parastomal bars and dorsal bridge of pharyngeal sclerite. 13. Cross section of ridges in floor of pharyngeal sclerite. 14. Dorsal view of pharyngeal ridges. Fig. 15. Egg. Abbreviations: AHB = anterior hypostomal bridge; DB = dorsal bridge; DC = dorsal cornu; HS = hypostomal sclerite; MH = mouthhooks; PB = parastomal bar; PhR = pharyngeal ridge; PS = pharyngeal sclerite; PHB = posterior hypostomal bridge; SpO = spiracular opening; VC = ventral cornu; W = window.

deeply pigmented ring. Segments 3–11 (Fig. 6) very similar, lateral margins indented and forming lateral and dorsolateral rows of low, bluntly rounded tubercles, lateral tubercles larger and bearing apical sensilla, each sensillum with 3–6 raylike processes, dorsolateral tubercles smaller, more bluntly rounded, and lacking apical sensilla; dorsal surface of each segment with clear areas near dorsolateral tubercles, each area bearing 2 scalelike structures; ventral surface of each segment (Fig. 7) with creeping welt of 2 rows of blackened spinules, spinules of more posterior row longer. Segment 12 bearing perianal pad ventrally and spiracular breathing tubes apicolaterally; perianal pad (Fig. 9) bilobed, each lobe bluntly rounded laterally, no post-anal spinule pad. Breathing tubes elongate, nearly 3 times as long as wide; each tube capped apically by spiracular plate, plates (Fig. 8) bearing 4 oval spiracular openings and 4 long, branched, hair-like processes.

Cephalopharyngeal skeleton (Fig. 10) length 0.37–0.40 mm, $\bar{x}$ = 0.39 (n = 5). Mouthhooks paired, not connected dorsally, narrow and sicklelike; hook part without accessory teeth along ventral border, basal part with elongate window and with narrow piece projecting posterodorsally. Hypostomal sclerite (Fig. 11) composed of lateral rods connected near midlength by 2 hypostomal bridges; anterior hypostomal bridge very narrow and barely detectable, strongly curved anteriorly; posterior bridge deeply pigmented, straplike. No epistomal sclerite. Parastomal bars (Fig. 12) arising from anterior border of pharyngeal sclerite, running forward above and somewhat between hypostomal sclerite, distal ends not connected and ending just above anterior margin of hypostomal sclerite. Pharyngeal sclerite mostly deeply pigmented; dorsal cornua thin, each with window posteroventrally, connected anterodorsally by dorsal bridge, bridge (Fig. 12) with 2 large windows posteriorly and 2 much smaller windows anteriorly; ventral cornua broad, each bearing large, poorly pigmented lobe anterodorsally; floor of pharyngeal sclerite bearing 9 broad, apically truncate ridges (Fig. 13), lateral ridges incomplete, all ridges lacking lateral lamellae and appearing broad and flat in dorsal view (Fig. 14).

DISCUSSION

In contrast to many species of Ephyridae, *L. excavata* seems to be a trophic specialist and to occur in more stable habitats. Perhaps the strong trophic specialization found in this species is its most distinctive characteristic. Zack and Foote (1978) reported that another common wetland ephyrid species, *Scatella stagnalis* Fallén, is very generalized trophically, as its larvae could utilize a broad spectrum of microorganisms. They reared larvae to adults on 13 different monocultures representing five classes of algae. Interestingly, larvae of *S. stagnalis* seem unable to utilize the blue-green algal genus *Cylindrospermum*, the preferred larval food of *L. exca-*

Table 4. Life history characteristics of *Scatella stagnalis* and *Lytogaster excavata*.

Characteristic	<i>S. stagnalis</i>	<i>L. excavata</i>
Adult longevity (days)	20-25	25±
Fecundity	500	30±
Developmental period (days)	10-14	21-29
Habitat stability	Low	High
Trophic niche	Broad	Narrow
Dispersal ability	High	Low

vata. The utilization of different algal foods may be one factor allowing for the coexistence of these two species in shoreline habitats.

As expected, *L. excavata* possesses certain life history characteristics that stand in direct contrast to traits displayed by such generalist species as *S. stagnalis* (Table 4). *Lytogaster excavata* has a slightly greater adult longevity, a greatly reduced fecundity, a distinctly longer developmental period, and a less motile larva than *S. stagnalis*. In addition, it usually occurs in habitats that are at least partially vegetated and less susceptible to perturbation by flooding, whereas *S. stagnalis* frequently is most abundant on open shoreline muds that are repeatedly and unpredictably inundated. In summary, *L. excavata* may be more of a K-selected "equilibrium" species, living in more stable habitats, whereas *S. stagnalis* is an r-selected "fugitive" species having high powers of dispersal that enables it to exploit quickly newly appearing spatial and trophic resources.

Blue-green algae are notably recalcitrant to grazing by phycophagous invertebrate animals (Arnold, 1971; Hargrave, 1970; Schindler, 1971). However, Foote (1977) reported that at least 12 species of Ephydriidae can utilize blue-greens. Most of these species belong to the Hyadini, and it appears that this tribe may be unified biologically by its ability to utilize this largely untapped food resource. This certainly holds true for species of *Axysta*, *Hyadina*, and *Lytogaster*, and perhaps for *Pelina*, as their larvae have been reared from field-collected colonies of blue-green algae (Foote, 1977). The three other North American genera that are usually placed in the tribe Hyadini, *Brachydeutera*, *Gastrops*, and *Ochthera*, have distinctly different larval feeding habits and perhaps should be re-evaluated as to their tribal placement.

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